Stream Macroalgae of the Hawaiian Islands: A Floristic Survey[1]

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Abstract: Between January 2001 and May 2003, 167 stream segments on the islands of Kaua'i, O'ahu, Maui, and Hawai'i were sampled for stream macroalgae and measured for a series of physical and chemical conditions. Conditions ranged more widely than previously reported, which is likely due to the greater diversity of habitats accessed and the year-round sampling representation in this study. Water temperature ranged from 12.5 to 27.5 °C (mean = 21.4 °C ± 2.4), pH from 5.5 to 8.9 (mean = 7.8 ± 0.5), and specific conductance from 20 to 490 $\mu S \cdot cm^{-1}$ (mean = 102 $\mu S \cdot cm^{-1}$ ± 75.9). A total of 160 specific and subspecific taxa was identified, of which 27 are new records for the Hawaiian Archipelago. The Chlorophyta compose the majority of the taxa, followed by the Cyanobacteria, Rhodophyta, Bacillariophyta, and Tribophyta. The mean number of taxa per stream segment was 5.0 ± 2.7, which is the highest such value reported. Grouping of taxa by morphological form demonstrates that the majority of taxa were free filaments (58%), followed by mats (17%), tufts (13%), and gelatinous colonies (9%). A principal coordinates analysis of the stream sites indicated that a high degree of overlap in floristic composition is evident for most of the Islands, and only sites on the island of Hawai'i exhibit a localized positioning to one side of the principal coordinates bi-plot. The flora of Hawai'i Island appears to be unique only in the sense that it contains fewer broadly distributed taxa than the remaining islands, which may be a function of island age. Cluster analysis of the islands based on two types of comparisons suggests stronger similarities between the islands of Maui and Kaua'i, and O'ahu and Hawai'i than previously reported. The Hawaiian stream macroalgal flora contains a number of cosmopolitan taxa, although it is recognized that concepts of some of these taxa may change with additional data.

LOCATED MORE THAN 3,500 km from the nearest continental landmass, Hawai'i is the most isolated archipelago in the world (Juvik and Juvik 1998). This chain of islands and atolls is recognized as an outstanding outdoor evolutionary laboratory due to a combination of extreme isolation, a broad range of available habitats, and a unique biota that has evolved following colonization by waif individuals (Juvik and Juvik 1998). Many organisms have been identified as examples of adaptive radiation in Hawai'i, including members of the angiosperms (which, as a group, are estimated to be 89% endemic) and the insect fauna (estimated to be 99% endemic) (Wagner and Funk 1995). The marine algae of the Hawaiian Islands are estimated to be 20–25% endemic, which is a moderate value for marine systems (Hawaiian marine systems are typically characterized by 25–35% endemism [Zeigler 2002]). Hawaiian marine algae have been actively studied for many years from a taxonomic perspective, culminating in the recent publication of several monographic works on Hawaiian red, green, and brown seaweeds (Abbott 1999, Abbott and

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Huisman 2004). Algae have also played an important role in Hawaiian culture. Edible algae, *limu* in the Hawaiian language, have been critical to the diet of native Hawaiian peoples for many hundreds of years (Abbott 1984). The vast majority of *limu* species are marine; however, a few freshwater and brackish examples are known, indicating that at least a few stream algae species were also culturally important (Abbott 1984). During the 1950s to the 1980s, a number of seaweed species were introduced to Hawai'i for production of compounds such as agar and carrageenan (Russell 1983, Rodgers and Cox 1999). Some alien species have since become naturalized in the Hawaiian flora, in several cases overwhelming the natural algal assemblages and growing to nuisance levels (e.g., Smith et al. 2002, 2004).

The freshwater algae of Hawai'i, by comparison, have received scarce attention over the past 130 yr. A bibliographic checklist of the nonmarine algae (freshwater and terrestrial) of the Hawaiian Islands indicates that 800 specific and subspecific taxa have been reported from Hawai'i (both microalgae and macroalgae), of which a mere 5.0% are believed to be endemic (Sherwood 2004). Knowledge of the stream macroflora of Hawai'i lags far behind that of the seaweeds, and only preliminary surveys discussing the taxonomic composition of stream algae are recorded in the published literature (e.g., Vis et al. 1994, Filkin et al. 2003, Sherwood et al. 2004). Still, these surveys highlight the great biodiversity in Hawaiian streams, as well as the potential for discovery of undescribed taxa. As an example, 25 of 34 taxa reported in the first survey of Hawaiian streams represented new records for the Archipelago, and one new species was described: the rhodophyte *Batrachospermum spermatiophorum* Vis & Sheath (Vis et al. 1994).

Determination of the native Hawaiian stream algal flora is virtually impossible. Such information is readily available for many other organismal groups, including angiosperms (e.g., Wagner et al. 1999), fishes (e.g., Randall 1996, Yamamoto and Tagawa 2000), and marine algae (Abbott 1999, Abbott and Huisman 2004). However, because the historical record of freshwater algae in Hawai'i is patchy at best, only an incomplete picture is available of the stream flora before the first Polynesian settlements (between AD 400 and 1100) and European contact (AD 1778) (Zeigler 2002). Although two ethnobotanical uses of brackish and freshwater algae are mentioned by Abbott (1984), the vast majority of *limu* are marine seaweeds, and the stream algal flora did not play nearly as important a role in the diet of native Hawaiians as the marine flora. It is almost certain that the stream algal flora was altered after human settlement of the Islands because the importation of animal species and cultivation of food crops from other Pacific islands could also have introduced freshwater and terrestrial algae species to Hawai'i. This scenario seems especially likely for cases such as drinking water and crop plants (which may have had soil surrounding the roots), brought by early Polynesians (e.g., Zeigler 2002). Two different approaches could be taken to infer the precontact stream algal flora, but neither is completely satisfactory. First, it could be assumed that the algae currently growing in pristine areas on each island represent refuge elements of the flora that were present before human contact and influence. Second, molecular genetic data could be used to pinpoint the divergence between congeners from possible colonization sources. Given the difficulty of such determinations, and the current lack of such data, this study makes no distinctions between taxa that may have been present in Hawaiian streams before human intervention and those that have since been introduced.

This study represents the most thorough survey of freshwater algae from Hawaiian streams. Algal stream surveys from other tropical as well as temperate areas over the last several decades have provided a comparative basis for this research (e.g., John and Moore 1985, Entwisle 1989, Necchi and Moreira 1995, Sheath and Cole 1996). The focus of the study reported here is on stream macroalgae; that is, those benthic algae that have a discrete thallus visible to the naked eye (Sheath and Cole 1992). Macroalgae are known to play an important ecological role

in stream systems in several ways. Stream macroalgae are important as a food source for native and endemic fishes in Hawaiian stream systems (Kido 1996) and are used both as food and structural materials by aquatic invertebrates in other geographic regions (Sheath et al. 1995, Keiper et al. 1998). Here, the results of a survey of 167 stream segments from the four main Hawaiian islands of Kaua'i, O'ahu, Maui, and Hawai'i are presented, with an examination of the floristic differences of the four islands.

MATERIALS AND METHODS

Field Procedures

Stream sites were accessed at roadside crossings, by day hikes to semiremote streams, or by helicopter drop-off collecting in high-elevation streams. At each sampling location, a 20-m stream segment was established and thoroughly searched for macroalgae using a glass-bottomed viewbox or a mask and snorkel. Site selection was heavily influenced by a combination of opportunity and accessibility. The majority of sites were accessible by road or hiking trail, and select high-elevation or remote coastal stream sites on the islands of O'ahu, Maui, and Hawai'i were sampled in coordination with other research teams. Detailed collection location information is available from A.R.S. (by request). At each site, all available substrata within the segment were examined, including rocks, sticks, and fallen trees, sediments, macrophytic vegetation, and dams or diversions. A representative sample of each macroalgal taxon was collected using long-handled forceps and fixed in a 20-ml scintillation vial with 2.5% $CaCO_3$-buffered glutaraldehyde, which is a suitable fixative for the retention of color and other morphological characteristics (Sheath et al. 1993).

A series of physical and chemical measurements was made at each site. Measurements included pH (using a waterproof pH meter [Oakton pHTestr 1]), specific conductance (using a portable meter [TDSTestr; 0–1990 $\mu S \cdot cm^{-1}$]), water temperature (using an alcohol pocket thermometer [FisherBrand]), current velocity (using a flow meter [General Oceanics or Global Water Flow Probe] or a floating bobber in very shallow segments), maximum depth (using a 200-cm folding rule [Lufkin]), and maximum width (using a 50-ft [15.24-m] reel tape [Keson]). Stream segments with a maximum depth of greater than 100 cm were noted as such but not measured. The color and clarity of the water were noted by eye at each site. Specific conductance, pH, and water temperature were measured in circulating but slow-flowing regions of the streams to allow the meters to stabilize. Current velocity was measured at three to five points across the stream (three points for narrow segments and five points for wide segments) and later averaged. Global Positioning System (GPS) readings, where taken, were made using a GPS receiver (Garmin E-Trex Summit [hand-held] or a Garmin GPAMap 76S, using the WGS84 positioning system). In many of the sampling locations included in the study, such as the back of steep-sided valleys, GPS reception was not available.

Laboratory Procedures and Data Analyses

Fixed macroalgae collections were refrigerated to retain sample color. Samples were identified using a combination of compound and dissecting microscopy. Both general and specific literature references were used to aid identification of taxa. General references included Smith (1950), Prescott (1951), Entwisle et al. (1997), Dillard (1999), John et al. (2002), and Wehr and Sheath (2003). Additional references were used for Cyanobacteria (Desikachary 1959, Anagnostidis and Komárek 1988, 1990, Komárek and Anagnostidis 1989), Chlorophyta (Islam 1961, 1963, van den Hoek 1963, Kadłubowska 1984, Mrozińska 1985), Rhodophyta (Necchi et al. 1993*a*,*b*, Sheath et al. 1993, Vis et al. 1994, Rintoul et al. 1999, Sherwood and Sheath 2000, Kumano 2002), Tribophyta (Ettl 1978), and Bacillariophyta (Patrick and Reimer 1966, 1975, Krammer and Lange-Bertalot 1991*a*,*b*, 1997*a*,*b*). Representative taxa were photographed using a compound microscope (Olympus BX-41) equipped with a digital camera (Olympus DP12).

Physical and chemical conditions mea-

sured at each stream segment were averaged by island to examine between-island differences. Taxa for each stream segment were compiled into species lists, and the total number of taxa from each was determined. Differences in the number of taxa per stream segment and physical/chemical conditions among islands were tested using one-way analysis of variance (ANOVA) with the Minitab v.12.1 statistical package (Minitab, Inc. 1998). The number of taxa in each broad taxonomic category (e.g., Cyanobacteria, Chlorophyta, Rhodophyta, Bacillariophyta, or Tribophyta) was determined and compared across islands to determine if similar proportions of taxa from each category were identified from each island. The mean number of taxa identified per stream segment was determined and compared with previous reports for Hawai'i and other geographic regions. Taxa were grouped into the following morphological forms following Sheath and Cole (1992) for comparison with other published stream surveys: mats, gelatinous colonies, gelatinous filaments, free filaments, tissuelike forms, tufts, and crusts.

Associations among stream sites based on the floristic data were examined using both cluster analysis and principal coordinates analysis (PCO). For the cluster analysis, the taxa were summed by island (Kaua'i, O'ahu, Maui, or Hawai'i) to indicate the number of identifications for each taxon, and the islands were clustered based on Sørensen's index using the Unweighted Pair Group Method using Arithmetic Averages (UPGMA) algorithm with the statistical software package MVSP (Multi-Variate Statistical Package [Kovach Computing Services 1986–1999]). For the PCO analysis, each stream segment was ordinated based on the presence or absence of each macroalgal taxon identified during the study, again using MVSP.

The number of endemic taxa and new records to the Hawaiian Islands were determined through comparisons with the literature (Sherwood 2004 and references therein). Records are here designated as new if previously unpublished (i.e., previously available only in the form of technical reports written by A.R.S.).

RESULTS

Summary of Stream Segments

The 167 stream segments surveyed from January 2001 to May 2003 included 36 from Kaua'i, 58 from O'ahu, 25 from Maui, and 48 from Hawai'i. Stream sites were largely localized on the windward side of islands because perennial streams in Hawai'i tend to be concentrated on that side due to orographic rainfall patterns (Giambelluca and Schroeder 1998). Thirteen of the 167 stream segments were turbid though colorless, and the remaining 154 segments were clear and colorless. Physical and chemical conditions of the streams varied by island but were also variable within islands (Figure 1). One-way ANOVA indicated significant differences among islands for water temperature, specific conductance, and maximum depth. Mean water temperature was lowest for Maui, due to the inclusion of a series of high-elevation sites from this island ($F = 11.32$, $df = 140$, $P < 0.001$). Water temperatures across the islands ranged from 12.5 to 27.5 °C (mean = 21.4 °C $\pm$ 2.4). Mean specific conductance was highest for O'ahu ($F = 6.89$, $df = 142$, $P < 0.001$), but this is consistent with the large proportion of urbanized sites on that island compared with the others, and specific conductance values ranged from 20 to 490 $\mu S \cdot cm^{-1}$ (mean = 102 $\mu S \cdot cm^{-1}$ $\pm$ 75.9). Maximum depth was most shallow on O'ahu and deepest on Kaua'i (range = 10–>100 cm; mean = 62.6 cm $\pm$ 33.8). Values for pH ranged widely for stream segments across the four main islands, but mean values ranged between 7.6 and 7.9 (mean = 7.8 $\pm$ 2.7). Mean current velocity and maximum width were also variable both within and among islands (Figure 1).

Taxonomic Analyses of Hawaiian Stream Macroalgae

In total, 160 different morphological taxa were identified from stream sites on the islands of Kaua'i, O'ahu, Maui, and Hawai'i (Table 1). This total comprises 57 Cyanobacteria, 84 Chlorophyta, seven Rhodophyta, seven Bacillariophyta, and five Tribophyta.

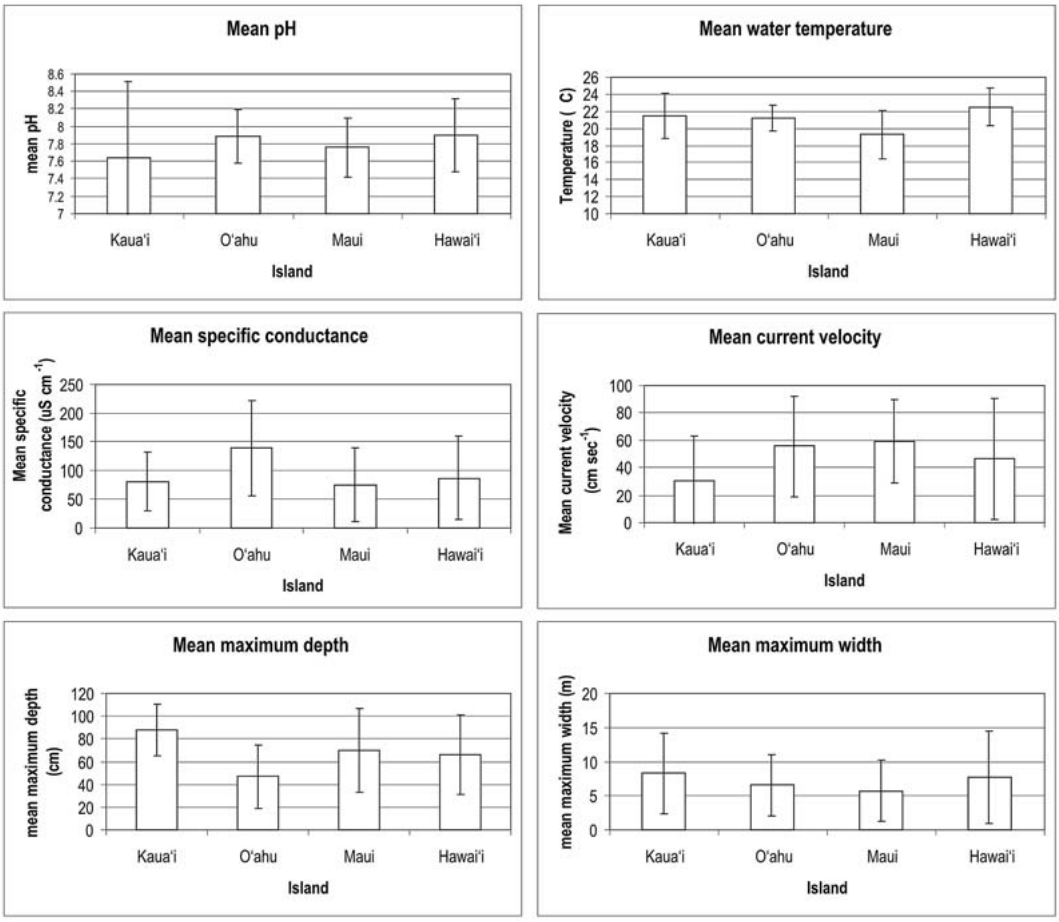

FIGURE 1. Graphical summary of physical and chemical conditions measured at stream sites, averaged by island (error bars illustrate standard deviations).

Representatives of several genera could not be identified to species because one or more morphological characteristics needed for species-level designation was missing from the collections (e.g., *Anabaena*, *Bulbochaete*, *Mougeotia*, *Oedogonium*, *Spirogyra*, and *Zygnema*). These are indicated only to the level of genus in Table 1. These morphological taxa were designated when some morphological or anatomical differences could be discriminated between collections, but at least one character required for species-level identification was missing. The greatest number of taxa was reported from O'ahu (81), followed by Hawai'i (69), Maui (60), and Kaua'i (59). Twenty-seven taxa are new records for Hawai'i (Table 1), adding to the 15 taxa recently reported as new records (Filkin et al. 2003). Only one species identified in the study reported here is endemic to Hawai'i (the red alga *Batrachospermum spermatiophorum* Vis & Sheath) (Table 1).

A comparison of the total number of taxa for the islands of Kaua'i, O'ahu, Maui, and Hawai'i indicates that approximately equal proportions of taxa from each broad taxonomic grouping were observed (Figure 2). In all cases, the Chlorophyta composed the largest number of taxa, with the Cyanobacteria as the second largest grouping. The

TABLE 1

Taxonomic List of Macroalgae Identified during This Study

Taxonomic Designation	Kaua'i	O'ahu	Maui	Hawai'i
Cyanobacteria				
Anabaena sp. (1 sp.)		X		
Calothrix braunii Born. & Flah.			X	X
C. fusca (Kütz.) Born. & Flah.			X	
Cylindrospermum stagnale (Kütz.) Born. & Flah.	X			
Cylindrospermum sp. (1 sp.)		X	X	X
Dichothrix baueriana (Grun.) Born. & Flah.			X	
‡*Geitlerinema splendidum* (Grev. ex Gom.) Anagn.		X		X
+*Hydrocoleum meneghinianum* Kütz.				X
‡*Leptolyngbya angustissima* (W. West & G. S. West)		X		
+*L. foveolarum* (Mont. ex Gom.) Anagn. & Komár.		X		
Lyngbya major Menegh.		X		
‡*Microchaete uberrima* N. Carter	X			
+*Microcoleus lacustris* (Rabenh.) Farlow ex Gom.		X		X
Nostoc commune Vauch.		X		
N. linckia (Roth) Born.	X			
N. paludosum (Kütz.) Born. & Flah.			X	X
+*N. pruniforme* (C. Ag.) Born. & Flah.	X	X	X	X
N. verrucosum (Vauch.) Born. & Flah.			X	
‡*Nostochopsis lobatus* Wood emend. Geitl.	X	X	X	
‡*N. radians* Bharadwaja	X	X		
‡*Oscillatoria limosa* (Roth) C. Ag.	X	X		X
O. princeps Vauch. ex Gom.				X
O. sancta (Kütz.) Gom.		X		
O. subbrevis Schmid.	X			
+*Phormidium ambiguum* Gom.	X		X	
‡*P. amoenum* Kütz.	X			
P. autumnale C. Ag. ex Gom.			X	
‡*P. corium* C. Ag. ex Gom.				
P. formosum (Bory) Anagn. & Komár.		X		
P. inundatum (Kütz.) Gom.		X		
P. pachydermaticum Frémy			X	
P. papyraceum (C. Ag.) Gom.	X			
P. putealis (Mont. ex Gom.) Anagn. & Komár.				X
P. retzii (C. Ag.) Gom.	X	X	X	X
+*P. stagnina* Rao		X		
P. subfuscum Kütz. ex Gom.		X	X	
+*P. subincrustatum* Fritsch & Rich		X		X
+*P. tinctorium* Kütz.	X	X		
P. truncicola Ghose	X	X		
Phormidium spp. (3 spp.)	X		X	
Pseudanabaena sp. (1 sp.)		X		
Rivularia haematites (D.C.) C. Ag.				X
R. minutula (Kütz.) Born. & Flah.	X			
Schizothrix rivularis (Wolle) Drouet	X			X
Scytonema arcangelii Born. & Flah.		X		X
‡*S. chiastum* Geitl.	X			
‡*S. coactile* Mont. ex Kütz.	X			
S. crispum (C. Ag.) Born.	X	X	X	X
+*S. fritschii* Ghose				X
S. rivulare Borzi			X	
S. tolypothricoides Kütz.	X			X
Stigonema mamillosum (Lyngb.) C. Ag. ex Born & Flah.				X
Tolypothrix distorta (Kütz.) Born. & Flah.		X		X
+*T. nodosa* (Kütz.) Born. & Flah.				X
T. tenuis (Kütz.) J. Schmidt		X		X

TABLE 1 (continued)

Taxonomic Designation	Kaua'i	O'ahu	Maui	Hawai'i
Chlorophyta				
[+]*Basicladia chelonum* (Collins) Hoffm. & Tilden		X		
[+]*Binuclearia tatrana* Wittr.	X			
Bulbochaete sp. (1 sp.)	X			
[‡]*Chaetophora elegans* (Roth) C. Ag.	X	X		
Chara braunii Gmelin		X	X	
Cladophora fracta (O. F. Müller ex Vahl) Kütz.		X		
C. glomerata var. *glomerata* (L.) Kütz.	X	X	X	X
C. glomerata var. *crassior* (C. Ag.) Hoek	X		X	X
Cladophora spp. (2 spp.)		X	X	
Cloniophora macrocladia (Nordst.) Bourr.	X	X		X
C. plumosa Kütz. emend. Bory	X	X	X	X
[+]*C. spicata* Schmidle emend. Islam	X	X	X	X
Cylindrocystis sp. (1 sp.)				X
Desmidium sp. (1 sp.)		X	X	X
Geminella minor (Näg.) Heering			X	X
[+]*Klebsormidium fluitans* (Gay) Lokhorst				X
[+]*K. subtile* (Kütz.) Tracanna ex Tell			X	
[‡]*Microspora pachyderma* (Wille) Lagerh.	X			
Mougeotia spp. (5 spp.)	X	X	X	X
Oedogonium sp. (15 spp.)	X	X	X	X
Oedogonium undulatum (Bréb.) A. Br.		X		
[+]*Rhizoclonium crassipellitum* W. West & G. S. West		X		
R. hieroglyphicum (C. Ag.) Kütz.	X	X	X	X
[+]*Schizomeris liebleinii* Kütz.		X	X	
[+]*Spirogyra dictyospora* C. C. Jao			X	
[+]*S. dubia* Kütz.			X	
[+]*S. elegantissima* Ling & Zheng		X		X
[+]*S. fallax* (Hansg.) Wille				X
S. fluviatilis Hilse				X
Spirogyra spp. (22 spp.)	X	X	X	X
[+]*Stigeoclonium fasciculare* Kütz.	X			X
S. flagelliferum Kütz.				X
[‡]*S. lubricum* (Dillw.) Kütz.	X	X	X	
[+]*S. pachydermum* Prescott	X			
[‡]*S. segarare* Islam	X			
S. setigerum Kütz.		X		X
S. stagnatile (Hazen) Collins		X	X	X
S. subsecundem (Kütz.) Kütz.	X	X		X
S. variabile Näg. ex Kütz.		X		
Ulothrix tenerrima Kütz.			X	
[‡]*U. tenuissima* Kütz.				X
Zygnema spp. (2 spp.)	X	X	X	X
Unknown desmid chain				X
Rhodophyta				
Audouinella sp. (1 sp.)	X	X	X	
A. eugenea (Skuja) C. C. Jao	X	X	X	
**Batrachospermum spermatiophorum* Vis & Sheath			X	
[+]*Chantransia* sp. (formerly *Audouinella chalybea* (Roth) Bory)				X
Chantransia sp. (formerly *A. pygmaea* (Kütz.) Weber-Van Bosse)	X	X		X
Compsopogon coeruleus (Balbis ex C. Ag.) Mont.	X	X	X	X
Hildenbrandia angolensis Welw. ex W. West & G. S. West	X	X	X	X
Bacillariophyta				
Cymbella turgidula Greg.		X		
Hydrosera whampoensis (Schw.) Duby	X	X	X	X
Melosira varians C. Ag.		X		X
[+]*Pleurosira laevis* (Ehrenb.) Compère	X	X	X	

TABLE 1 (continued)

Taxonomic Designation	Kaua'i	O'ahu	Maui	Hawai'i
Synedra ulna (Nitzsch) Ehrenb.	X	X	X	X
Tabellaria flocculosa (Roth) Kütz.	X	X		X
Terpsinöe musica Ehrenb.		X	X	
Tribophyta				
Tribonema aequale Pasch.				X
T. elegans Pasch.	X			
Tribonema sp. (1 sp.)		X		
[+]*Vaucheria* spp. (2 sp.)		X	X	

Note: The distribution of each taxon is summarized by island. Taxa believed to be endemic to the Hawaiian Islands are indicated with an asterisk (*), and new records to Hawai'i are indicated with [+]. Those recently reported as new records by Filkin et al. (2003) are noted by [‡].

Rhodophyta, Bacillariophyta, and Tribophyta each accounted for a much smaller proportion of the total taxa than the first two groups (Figure 2). Grouping the flora by morphological form indicates that the assemblage is composed of 93 free filaments, 27 mats, 21 tufts, 14 gelatinous colonies, two gelatinous filaments, two tissuelike forms, and one crust.

The most widely distributed taxa (i.e., identified from streams on all islands in the study) are *Nostoc pruniforme* (C. Ag.) Born. & Flah., *Phormidium retzii* (C. Ag.) Gom., and *Scytonema crispum* (C. Ag.) Born. (Cyanobacteria); *Cladophora glomerata* (L.) Kütz., *Cloniophora plumosa* Kütz. emend. Bory, *C. spicata* Schmidle emend. Islam, *Rhizoclonium hierogylphicum* (C. Ag.) Kütz., *Spirogyra* spp., *Oedogonium* spp., *Mougeotia* spp., and *Zygnema* spp. (Chlorophyta); *Compsopogon coeruleus* (Balbis ex C. Ag.) Montagne and *Hildenbrandia angolensis* Welw. ex W. West & G. S. West (Rhodophyta); and *Hydrosera whampoensis* (Schw.) Duby and *Synedra ulna* (Nitzsch) Ehrenb. (Bacillariophyta).

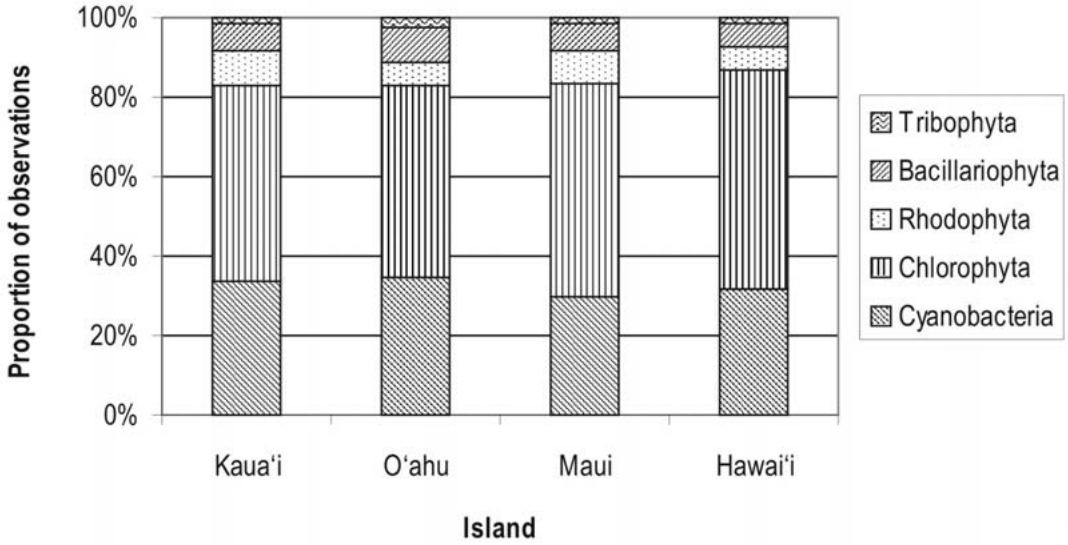

FIGURE 2. The proportion of identifications from each island represented by each broad taxonomic category (Cyanobacteria, Chlorophyta, Rhodophyta, Bacillariophyta, and Tribophyta).

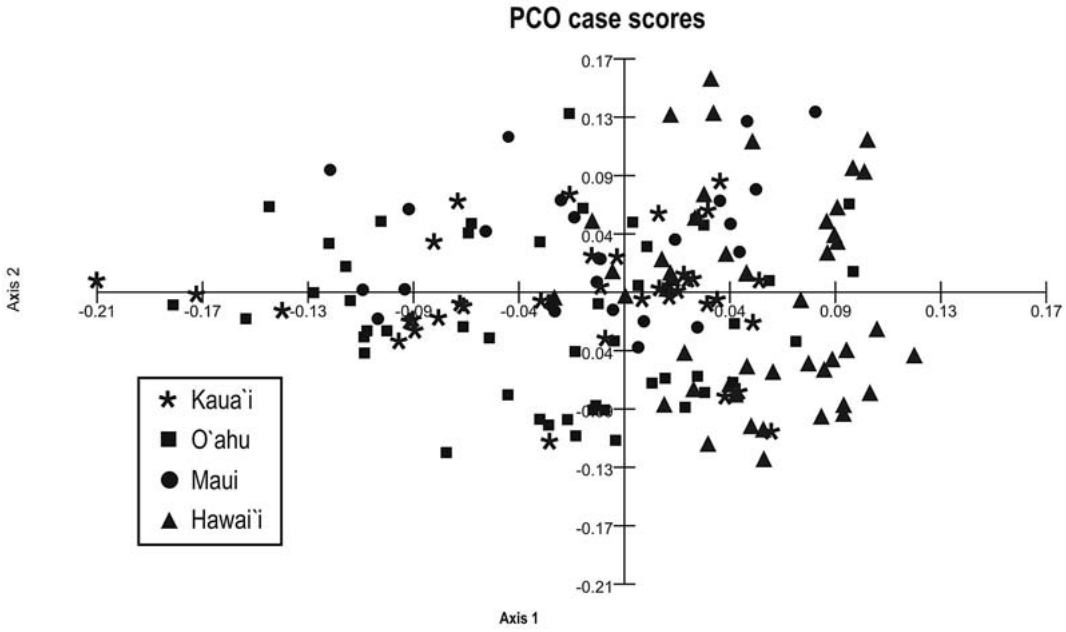

FIGURE 3. Principal coordinates analysis bi-plot of stream sites, based on presence or absence of each taxon identified during the entire study. The first principal coordinates axis accounts for 7.9% of the variation, and the second accounts for 6.9%. The distribution of sites on the plot indicates that the islands display considerable overlap in their taxonomic composition of stream algae, although sites on Hawai'i Island are more localized on the right side of the plot.

Floristic Analyses of Hawaiian Stream Macroalgae

A principal coordinates analysis of stream sites based on the taxa was performed to determine whether the sites were associated by island (Figure 3). The analysis was performed using the presence or absence of each taxon for each stream segment. Stream sites on the bi-plot are coded by island, and their positioning indicates that the four main islands do not have distinctive floras, as illustrated by the high degree of overlap (Figure 3). Data points representing stream segments from the islands of Kaua'i, O'ahu, and Maui are broadly distributed, although those from O'ahu are positioned with the greatest coverage on the bi-plot (Figure 3). Data points from streams on the island of Hawai'i, however, demonstrate slightly more clustering than those for the other three islands and are located primarily on the right-hand side of the bi-plot (Figure 3).

A cluster analysis of the four main islands was performed by summing the total number of taxa on each island and clustering based on Sørensen's similarity index (Figure 4) to directly compare the results with those from a previous study of Hawaiian stream macroalgae using this algorithm (Vis et al. 1994). The analysis indicates clustering of the island groups of Maui and Kaua'i, and O'ahu and Hawai'i, albeit at low similarity values.

The mean number of taxa identified per stream segment was highest for Maui (5.7), followed by Hawai'i (5.4), O'ahu (4.8), and Kaua'i (4.3). Overall, the mean number of taxa identified per segment was 5.0 ± 2.7, with a range of 1–15. The number of taxa identified only from a single island was determined to investigate whether some islands are inhabited by a greater number of unique taxa than others. The greatest number of unique taxa was identified from the island of O'ahu (31), followed by Maui (23), Hawai'i (21), and Kaua'i (20).

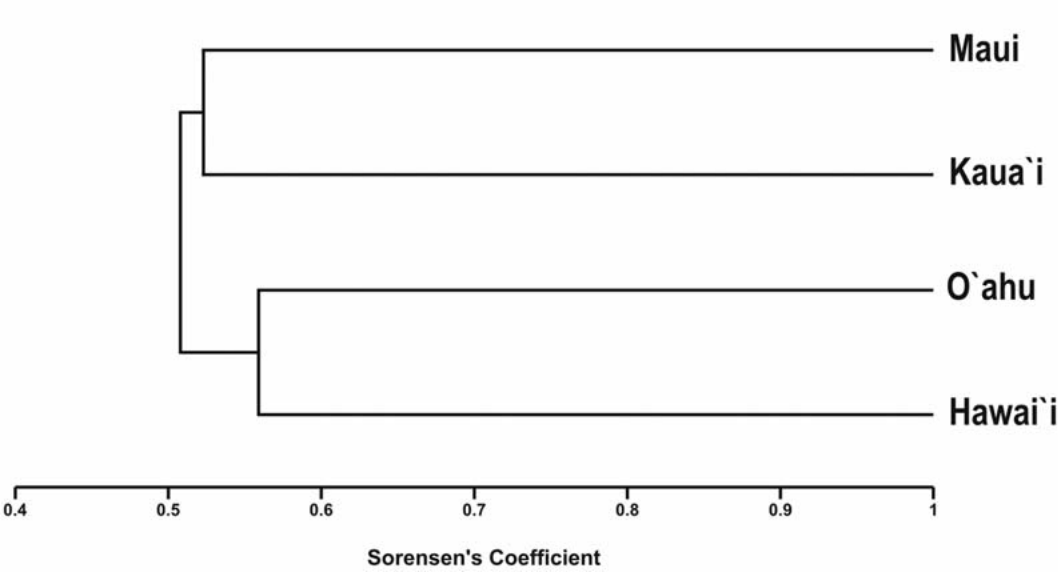

FIGURE 4. Cluster dendrogram of the Hawaiian Islands sampled during the study based on Sørensen's similarity index and the UPGMA algorithm (shared presence or absence of each taxon on each island).

DISCUSSION

The measured physical and chemical conditions of stream sites in this study were similar to those reported in previous surveys, although with a larger range, which is almost certainly due to the broader variety of stream sites accessible, as well as the year-round representation in sampling. For example, Vis et al. (1994) reported water temperatures from 20–27 °C, and Filkin et al. (2003) reported 17–24 °C, whereas the survey reported here included measurements from 12.5–27.5 °C, with the lowest values being measured from high-elevation streams on the island of Maui. Values for pH ranged between 5.5 and 8.9, in contrast to a range of 6.7–8.0 for Vis et al. (1994) but identical to the range reported by Filkin et al. (2003). The range of specific conductance values reported in this study (20–490 $\mu S \cdot cm^{-1}$) is larger than for previous surveys (20–360 $\mu S \cdot cm^{-1}$ [Vis et al. 1994, Filkin et al. 2003]) and may be due to the inclusion of some heavily urbanized sites and agricultural streams.

The 160 morphological taxa identified in this study greatly increase the known number of macroalgae in Hawaiian stream systems. The only previous studies to concertedly examine macroalgae in Hawaiian streams reported 34 and 42 taxa across the Islands (Vis et al. 1994, Filkin et al. 2003, respectively), most of which (91%) were also identified in the survey reported here. A comparison with a comprehensive survey of over 1,000 stream segments from North America and the Caribbean indicates that 44% of the taxa reported in the study reported here were also identified from the North American continent (Sheath and Cole 1992), although only 100 of the 160 taxa in this survey were identifiable to the species or subspecific taxonomic level, meaning that 38% of taxa in the study reported here were excluded from the comparison. A comparison of these results with a study of the stream macroalgae of Fiji (Sheath and Cole 1996) indicates that the flora of the Hawaiian Islands is relatively speciose. Only 15 species were identified from Fiji (11 of which were also identified from Hawai'i), with a mean number of taxa per segment of only 2.6 (in contrast to 5.0 ± 2.7 for Hawai'i) (Sheath and Cole 1996). Lobban et al. (1990) conducted stream surveys on Yap and Guam and identified 23 macroalgal taxa

from a total of 36 sites. Of these, 10 taxa were common to Hawai'i, a substantial proportion (Lobban et al. 1990). Necchi and Moreira (1995) reported 12 macroalgal taxa from two tropical streams in São Paulo State, southeastern Brazil, of which six are also identified in the study reported here. In contrast, comparisons with more temperate regions indicate less affinity with the Hawaiian flora. A survey of the Yarra River basin in southeastern Australia revealed a total of 43 taxa, of which 13 are in common with Hawai'i (Entwisle 1989), and a study of the River Thames in southern England reported 19 taxa, of which five are also found in Hawai'i (John and Moore 1985).

Of the taxa identified in this study, 58% were morphologically classified as free filaments, 17% were mats, 13% were tufts, 9% were gelatinous colonies, and the remaining 3% were gelatinous filaments, tissuelike forms, and a single crust. This contrasts to the earliest Hawaiian stream macroalgae survey, which reported a twofold number of mats over free filaments but similar proportions of the remaining morphological forms (Vis et al. 1994). The North American continental survey by Sheath and Cole (1992) also reported mats to be the most common morphological form (42%), followed by gelatinous colonies (23%), and gelatinous filaments (13%). Thus, the findings of the study reported here indicate that Hawaiian streams have a larger proportion of free-filament morphological forms than found in North American mainland streams.

The mean number of taxa identified per stream segment varied by island from 4.3 to 5.7, with an overall mean of 5.0 ± 2.7 taxa per segment. Similar calculations for the Sheath and Cole (1992) survey of North American streams yielded a mean of 3.1 taxa per segment, with a range from 0 to 11. The two previous surveys of Hawaiian stream macroalgae also reported higher values than the North American survey (mean of 3.4 taxa per segment by Vis et al. 1994 and 3.9 by Filkin et al. 2003).

The PCO analysis indicates that there is a large degree of overlap in the macroalgal floras of the four main Hawaiian Islands. Only the sampling sites from the island of Hawai'i have a distribution pattern that is concentrated in any manner (Figure 3). Explanation for this trend is not obvious. Although habitats for the streams on each of the islands varied somewhat in elevation and degree of urbanization, they were almost all concentrated on the wet, windward side of the islands (due to orographic rainfall patterns). The one exception may be two high-elevation bog sites from the island of Kaua'i (Kaua'i 59 and 61), which had very low pH and specific conductance values and also contained few species (two and four taxa, respectively). Examination of the number of "unique taxa" to each island (i.e., taxa identified only from a single island) reveals that Hawai'i Island has the second lowest number of unique taxa (20, as opposed to 19 for Kaua'i, 31 for O'ahu, and 22 for Maui). However, if these numbers are standardized by the number of stream segments analyzed from each island to yield a rate of unique taxa per stream segment for each island, it can be seen that actually Hawai'i has the lowest number of unique taxa per site (0.408), followed by Kaua'i (0.528), O'ahu (0.556), and Maui (0.880). Hence, one possible explanation for the slightly different distribution of Hawai'i island stream sites on the PCO bi-plot is that this island is distinctive in having fewer "unique taxa," or, worded another way, the macroalgal flora of Hawai'i Island tends to have a broader interisland distribution than that of the other islands. This is not unreasonable considering that the Big Island is the youngest of the Hawaiian Islands, with a volcanic age of 0–0.6 million yr (my), which contrasts with 1.2–1.5 my for Maui, 2.6–3.0 my for O'ahu, and 4.7 my for Kaua'i (Price 2004).

The cluster analysis of the main Hawaiian Islands according to their macroalgal floras indicated similar trends in the PCO analysis (Figure 4). Maui and Kaua'i clustered together based on floristic composition, as did O'ahu and Hawai'i. This pattern differed slightly from that demonstrated by Vis et al. (1994), based on a similar analysis (using Sørensen's similarity index), where the islands of Kaua'i and O'ahu are most similar,

followed by Maui, and finally the island of Hawai'i.

It is notable that despite the paucity of published surveys of Hawaiian stream algae, very few undescribed taxa were identified during this study. Thus, based on the available data, the Hawaiian stream macroalgal flora appears to be mostly cosmopolitan with many taxa known from other tropical and subtropical locations and some even from outside the tropics altogether (e.g., the cyanobacterium *Phormidium retzii* and the green alga *Cloniophora spicata* [Islam 1961, Sheath and Cole 1992]). However, the stream macroalgal identifications reported in the study reported here are based solely on the morphology of the taxa, and it is recognized that the taxonomic designations may change if other data highlight greater diversity than is conveyed through the relatively simple morphology of the algae (i.e., molecular phylogenetic data or life history observations). An example from the Hawaiian flora is the widespread cyanobacterium *Phormidium retzii*, which is also recognized as one of the most widely distributed macroalgal taxa throughout North America and the Caribbean and is relatively common in European streams (Sheath and Cole 1992). Based only on morphology, *P. retzii* appears to be a very cosmopolitan species, but recent molecular analyses indicate that the taxon likely represents a large species complex (Casamatta et al. 2003). Thus, *P. retzii* from Hawai'i may also contain a number of distinct species that simply are not morphologically distinguishable. The only study to date of Hawaiian stream macroalgae including molecular data is a phenologic and phylogenetic study of the endemic red alga *Batrachospermum spermatiophorum* (Sherwood et al. 2004), which confirmed the endemic status of the species by comparison of *rbc*L gene sequence data with worldwide congeners. The Hawaiian representatives of the marine red algal order Nemaliales have recently undergone substantial revision based on combinations of anatomical and molecular data (e.g., Huisman et al. 2003, 2004*a*,*b*), and many changes may also be forthcoming for the freshwater flora following similar kinds of studies. Specifically, several potentially undescribed taxa were collected during the survey reported here (e.g., two *Phormidium* taxa and two *Cladophora* taxa). Full taxonomic analysis of these collections, including DNA sequence comparisons or other molecular techniques in conjunction with more traditional kinds of data, may result in an augmented recognized diversity.

As the most comprehensive survey of Hawaiian stream macroalgae to date, this study provides a basis for future investigations of phylogeny, biogeography, and population genetics of this group. Several lines of research should be investigated to more fully understand the origins and evolution of these organisms in this isolated archipelago, including the mechanisms of arrival of the first waif individuals, the order and frequency of colonization of the main islands, and the degree of molecular diversification both within the Hawaiian Islands and in comparison with continental and other tropical Pacific island floras.

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